

# EMBRYOLOGY OF CHRYSOTHAMNUS (ASTEREAE, COMPOSITAE)

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Embryological information is scanty on the wide-spread *Chrysothamnus* of western America. "Embryology" is used here in its broad sense, following Davis (1966) and others. Snow (1945) reported details of gametogenesis for a population referable to *C. nauseosus* (Pallas) Britt. ssp. *albicaulis* (Nutt.) H. & C. Although gametogenesis is similar in some other subspecies of *C. nauseosus*, it certainly is not homogeneous throughout the genus. Embryological data on all species of *Chrysothamnus* are recorded here as part of an intensive study (Anderson, 1970) on the floral anatomy of the genus. Those features of embryology that characterize the genus or the entire family are treated only briefly.

## METHODS AND MATERIALS

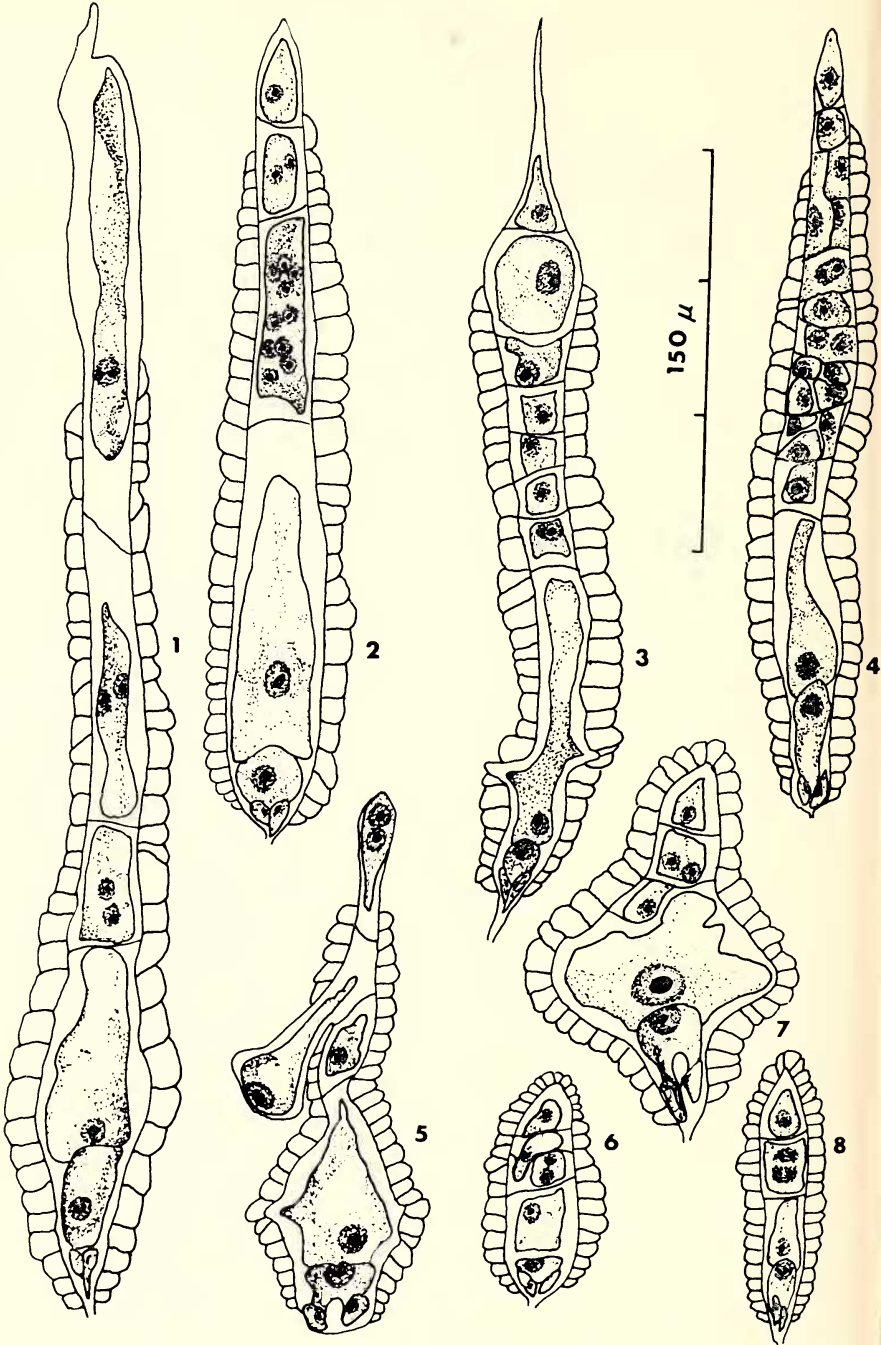
Over 90 populations were studied. Most materials were preserved in FPA in conjunction with general anatomic studies. That fixative was acceptable but caused considerable shrinkage in the embryo sacs. Killing heads in Craff V (Sass, 1958) resulted in much better preservation. Fixed tissues were dehydrated in a graded TBA series, embedded in paraplast, and cut at 9–12 $\mu$ , depending on age of the flowers. Sectioned tissues used in general studies were stained in safranin-fast green with tannic acid-ferric chloride mordanting. Tissues prepared specifically for this study were stained in Harris hematoxylin followed by fast green and mounted in permount. Many of the slides were prepared by Kent Fish.

## EMBRYOLOGY

Growth of flowers in one head is closely synchronized. Although individual flowers develop acropetally on the receptacle (Snow, 1945), they usually undergo either microsporogenesis or megasporogenesis simultaneously regardless of differences in individual flower size. The least synchronous species is *C. linifolius* Greene. In it, older flowers of the head have mature embryo sacs when the youngest flower undergoes meiosis in the ovule.

Anthers in *Chrysothamnus* are tetrasporangiate. Method of wall formation is the dicotyledonous type (Davis, 1966) with a glandular tapetum. Many aspects of microsporogenesis have been considered earlier (Anderson, 1966).

The ovules are anatropous, unitegmic, and tenuinucellar. Four cellular megaspores result from meiosis. The chalazal megaspore usually pro-



duces the embryo sac; however, a functional micropylar megaspore was observed in one sample of *C. linifolius* (Anderson 2738, KSC). The nucellus is intact at the tetrad stage but breaks down concurrently with three megaspores before the enlarged functional megaspore divides. On disintegration of the nucellus, an endothelium (integumentary tapetum) develops; its cells are often binucleate.

Taxa of *Chrysothamnus* develop a Polygonum type embryo sac. Mature embryo sacs (figs. 1–8) are typically long and narrow. The longest observed (fig. 1) was  $495\mu$  (44% of total ovule length at that age). In most samples embryo sacs range from 150–300 $\mu$  (15–20% of total ovule length). The wider embryo sac shown in fig. 7 probably is a post-fertilization condition.

The synergids are somewhat vacuolated and usually extend into the micropyle, especially in *C. nauseosus* (fig. 7). The egg is characteristically overarched by the central cell (figs. 2, 7) in which the polar nuclei fuse prior to fertilization. Average antipodal size is 20–30 $\mu$ . The largest is usually the chalazal antipodal, over 200 $\mu$  in *C. viscidiflorus* (Hook.) Nutt. ssp. *lanceolatus* (Nutt.) Piper (fig. 1) and *C. viscidiflorus* ssp. *puberulus* (D.C.Eat.) H. & C. The largest basal antipodal observed was 80 $\mu$  (fig. 2). Occasionally, one of the interstitial antipodals is the largest, but never over 50 $\mu$  long.

The antipodal apparatus in the megagametophyte varies widely. Three trends were observed: 1, antipodal cells reduced to two, one with two nuclei (fig. 8); 2, nuclei multiplied so that one or more of the three antipodals are multinucleate (fig. 2), and some individual nuclei may be multinucleolate; 3, divisions continued to more than three antipodals (fig. 3). The last two trends are interrelated; several antipodals may be present with one or more multinucleate (fig. 4). Antipodal cell number and frequency for all species are listed in Table 1.

In the Compositae, antipodal multiplication often results in persistent, haustorial cells (Davis, 1966). In *Chrysothamnus*, truly haustorial antipodals are infrequent. A strong lateral haustorium was observed only in *C. viscidiflorus* ssp. *humilis* (Greene) H. & C. (fig. 5). An indication of a weak lateral haustorium was seen in *C. linifolius* (fig. 6). The production of an haustorium by elongation of the chalazal antipodal (figs. 1–5) is more frequent than lateral haustoria. If the chalazal antipodal surpasses the endothelium, it is considered haustorial. Nonetheless, haustorial activity is not prolonged in *Chrysothamnus* because the antipodals usually become inactive and disintegrate shortly after fertilization or

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FIGS. 1–8. Mature embryo sacs and endothelium in *Chrysothamnus*: 1, *C. viscidiflorus* ssp. *lanceolatus* (Anderson 2717, KSC); 2, *C. nauseosus* ssp. *leiospermus* (Anderson 1995, KSC); 3, *C. pulchellus* (Anderson 3213, KSC); 4, *C. parryi* aff. ssp. *nevadensis* (Anderson 2966, KSC); 5, *C. viscidiflorus* ssp. *humilis* (Anderson 2950, KSC); 6, *C. linifolius* (Anderson 2500, KSC); 7, *C. nauseosus* ssp. *nauseosus* (Anderson 2707, KSC); 8, *C. viscidiflorus* ssp. *viscidiflorus* (Anderson 2900, KSC).

TABLE 1. NUMBER OF ANTIPODALS AND THEIR OBSERVED FREQUENCY IN EMBRYO SACS IN CHRYSOTHAMNUS.

	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<b>NAUSEOSI</b>															
<i>C. parryi</i>		2	8	7	7	4	3	1	1	1	2	1			1
<i>C. nauseosus</i>		6	5	8	5	3	3	2	2		2				
<b>CHRYSOTHAMNUS</b>															
<i>C. linifolius</i>			3	1	1	1									
<i>C. spathulatus</i>			1	1											
<i>C. albidus</i>	1	2	1												
<i>C. greenei</i>		2	4			2	1								
<i>C. viscidiflorus</i>	3	11	7	6	4	3									
<b>PULCHELLI</b>															
<i>C. vaseyi</i>		2	2	1											
<i>C. molestus</i>			4	1											
<i>C. depressus</i>		1	1	1	1										
<i>C. pulchellus</i>				1	1	1									
<b>PUNCTATI</b>															
<i>C. paniculatus</i>	1	3	1	1										1	1
<i>C. teretifolius</i>		2	1												

occasionally prior to fertilization as in *Anderson 2927* (KSC, *C. nauseosus* ssp. *albicaulis*). Relatively persistent chalazal haustoria were found in *C. albidus* (Jones) Greene and *C. greenei* (Gray) Greene.

Shortly after fertilization the embryo sac becomes laterally distended in all taxa (as in fig. 7). Embryogeny is the asterad type. Endosperm formation is nuclear at first. Further growth precipitates wall formation that progresses to form a cellular endosperm.

#### DISCUSSION

Size of embryo sacs in *Chrysothamnus* varies widely. Extremes (figs. 1, 8) are found in *C. viscidiflorus*, the only species known to contain polyploids (Anderson, 1966). Polyploidy evidently has no significant bearing on embryo sac size; the largest as well as the smallest come from diploids.

Howe (1959) found lateral haustoria in species of *Grindelia*, *Gutierrezia*, and *Haplopappus*. He used that phenomenon (less frequent than chalazal haustoria in Astereae) to suggest interrelationship of the taxa. Nevertheless, the presence of a lateral haustorium in *C. viscidiflorus* ssp. *humilis* does not suggest that it is related to those taxa also. It does, however, point to the distinctness of that taxon. In fact, unique features in its floral anatomy reinforced my decision to recognize it as a separate species (Anderson, 1970).

Species are listed in table 1 in a phylogenetic sequence (assumed from gross morphology). Patterns in antipodal numbers are fairly well in accord within sections, except for the unusual bimodal pattern in *C. paniculatus* (Gray) Hall. In section *Chrysothamnus*, and particularly in the *Pulchelli*, the average number reflects the assumed phylogeny.

Antipodal apparatus in *Nauseosi* is especially interesting as both species of that section are considered primitive and have numerous subspecies. In a statistical study of floral features (Anderson and Fisher, in press) *C. parryi* (Gray) Greene ssp. *parryi* was determined the most primitive taxon in the genus. If the postulate that an antipodal number of three is primitive, it is noteworthy that embryo sacs in *C. parryi* ssp. *parryi* usually have five to seven antipodals. The more primitive taxa of *C. nauseosus* have megagametophytes with three to five antipodals. In both species the higher numbers of antipodals are found in taxa adapted to xeric environments. If that is a trend, it is not universal; in section *Chrysothamnus*, *C. albidus* and *C. viscidiflorus* with two to three antipodals are fairly well adapted to xerism.

Hall (Hall and Clements, 1932) stated *C. paniculatus* was the most stable and primitive species in the genus. Its uniformity in external morphology is not seen in its embryology. Contrary to Hall's view, that species is very specialized (table 1). I had considered it less so than *C. teretifolius* (Dur. & Hilg.) Hall; however, embryological information reinforces a more recent determination (Anderson and Fisher, in press) that it is more specialized.

The close similarity of the *Punctati* to *Haplopappus*, section *Ericameria* (Anderson, 1966), now includes their embryology. *Haplopappus propinquus* Blake (*Raven 16802*, RSA) has four antipodals in the megagametophyte, and *H. trianthus* Blake (*Anderson 3032*, KSC) has five. Similarly, the *Nauseosi* are close to *Haplopappus*, section *Macronema* (Anderson and Reveal, 1966); *H. macronema* Gray from California (*Anderson 2922*, KSC) has five to seven antipodals, and another population from Colorado (*Anderson 2540*, KSC) has 10 antipodals.

In the Astereae, a multinucleate antipodal apparatus is known for several genera related to *Chrysothamnus*; i.e., *Haplopappus* (Harling, 1951), *Petradoria* (Anderson, 1963), and *Solidago* (Beaudry, 1958). In none, with the possible exception of *Haplopappus*, is the latitude of variability in the megagametophyte so great as it is in *Chrysothamnus*.

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TWO NEW SPECIES OF LAMOIROUXIA  
(SCROPHULARIACEAE) IN MEXICO

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The genus *Lamourouxia* H. B. K., nom. cons. (Taxon 18: 479-480. 1969), allied to the Rhinanthoideae of Scrophulariaceae, is distributed from northern Mexico through Central America to South America about as far south as Lima, Peru. Of the approximately 26 species, the following two have been studied jointly. They are placed in section *Hemispadon* Bentham, having long tubular, red corollas with a pair of large anthers and a pair of sterile staminal filaments. Search through the literature and at least 25 herbaria, including the major ones of Europe, has failed to disclose other names or collections for these two species. They are being described here to make the names available before a taxonomic revision and a discussion of their morphological relationships to avoid a longer author citation.

***Lamourouxia colimae*** Ernst & Baad, sp. nov. Herba suffruticosa, erecta. Folia glabriuscula, elliptica vel ovata, paucis dentata, attenuata basin versus, nervatura supra impressa. Calyx glaber, limbis patulis, late triangulatis. Corolla coccinea, cylindrica, labio superiore bifido, lobis rotundatis parum cuspidatis, non vel minime reflexis, labio inferiore